

LEAF BLIGHT of

Tomato and Potato Plants

Factors Affecting the Degree
of Injury Incited by
Alternaria dauci f. solani

John B. Rowell



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WHAT THIS BULLETIN IS ABOUT

Successful planning of military strategy requires a thorough knowledge of the enemy. Similarly, plant scientists must have all possible information to plan control measures against plant disease. This bulletin reports studies evaluating the capacity of *Alternaria dauci* f. *solani* to cause leaf blight of tomato and potato plants.

Two aspects of the disease were investigated; (1) the attack potential of the fungus pathogen, and (2) the defensive mechanisms of the plant hosts. Different degrees of virulence were found among races of the pathogen. Two types of resistance, permanent and temporary, were found in host plants, but only the latter occurred in commercial varieties of potatoes and tomatoes. This defensive mechanism exists in young foliage but was lost as the plants matured. The loss was related to the changes that occur in plant sugars. Thus, plant tissues that were aged, shaded, or treated with excessive amounts of certain agricultural chemicals became severely diseased.

Practical application to prevent destructive losses caused by *A. dauci* f. *solani* can be made of the basic information in this bulletin. For example, the fungus often causes serious injury as collar rot in tomato transplants during transit from southern states to northern growers. The transportation period favors the changes in storage carbohydrates which make the seedlings more prone to disease. This report suggests that such losses could be prevented by seedling treatment with sucrose prior to shipment.

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LEAF BLIGHT OF TOMATO AND POTATO PLANTS—

Factors Affecting the Degree of Injury Incited by *Alternaria dauci f. solani*

John B. Rowell*

INTRODUCTION

Early blight caused by *Alternaria dauci* (Kühn) Groves and Skolko *f. solani* (E. and M.) Neergaard is generally the principal defoliation disease on potato and tomato crops in northern United States when late blight caused by *Phytophthora infestans* (Mont.) DeBary is absent or non-epidemic. Frequently the most severe attacks occur late in the season when the host plants have matured. The older tissue of the lower leaves has been noted to be more susceptible than the younger tissue of the topmost leaves by Rands (19) and Bonde (3). Therefore, *A. dauci f. solani* is generally considered only a weak pathogen of old senescent tissues.

Nevertheless, the early blight pathogen also causes collar rot on the stems of young tomato plants and can attack the foliage of young potato and tomato plants under favorable environmental conditions. These inconsistencies in the host-pathogen relationship indicate the dependence of disease development on certain phases of host physiology which have not been thoroughly investigated.

The present study is concerned with certain factors that affect the pathogenicity of *A. dauci f. solani* in early blight, the defoliation disease of tomato and potato. Pathogenic races and host physiology were investigated to determine their relation to disease development in young and old foliar tissues.

The literature on the early blight pathogen has been thoroughly reviewed by Neergaard (16), with particular emphasis on the morphology and taxonomy of the fungus. Only recent nomenclatorial changes will be summarized here. Groves and Skolko (8) established *A. brassicae* (Berk.) v. *dauci* Lindau, the pathogen of carrot leaf

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blight, to be distinct from *A. brassicae* and raised it to specific rank as *A. dauci* (Kühn) Groves and Skolko. These authors also noted the similarity between this species and *A. solani* (E. and M.) Jones and Grout. Earlier, Angell (1) had noticed the similarity of morphological and cultural characters of *Macrosporium porri* Ell., the pathogen of purple blotch of onion, and *A. solani*, and he considered them to be physiologic races of the same species but did not change their nomenclature. Neergaard (16) compared these three species culturally, morphologically, and pathogenically and found distinctive differences only in the latter characteristic; accordingly he combined *A. solani* and *M. porri* under *A. dauci* (Kühn) Groves and Skolko as two *formae specialis*, *A. dauci* f. *sp. porri* (E11.) Neergaard and *A. dauci* f. *sp. solani* (E. and M.) Neergaard.

MATERIALS AND METHODS

The cultures of *Alternaria dauci* f. *solani* used in this study were monoconidial isolates derived from diseased material collected in Minnesota and Rhode Island. Cultures were labeled with three symbols, the first numeral designated the source, the letter indicated the order of isolation (numbers 1 to 8 were first obtained as mass cultures) and the last numeral represented the single-spore isolate number. The sources of the original diseased specimens are listed in Table 1.

TABLE 1. Sources of original cultures of *Alternaria dauci* f. *solani*.

Number	Host	Location	Date isolated
1.*	Potato	University Farm, St. Paul, Minn.	3-6-44
4.*	Potato	Cambridge, Minn.	3-6-44
5.*	Potato	Cambridge, Minn.	3-6-44
8.*	Potato	East Grand Forks, Minn.	3-23-46
13.	Potato	Brooklyn Center, Minn.	8-1-46
16.	Tomato	Brooklyn Center, Minn.	1-24-47
17.	Potato	Elk River, Minn.	1-24-47
18.	Potato	East Grand Forks, Minn.	1-24-47
19.	Potato	East Grand Forks, Minn.	1-24-47
22.	Potato	Kingston, R. I.	8-28-47
23.	Tomato	Kingston, R. I.	8-28-47
24.	Potato	Tuckertown, R. I.	9-8-48

*Cultures supplied by C. J. Eide.

A. dauci f. *solani* sporulates sparingly under the usual conditions of laboratory culture. The extensive and contradictory literature on the methods of inducing sporulation of *A. dauci* and its two forms in culture has been summarized by Neergaard (16). Comparisons of the different techniques using various strains of *A. dauci* f. *solani* demonstrated that a combination of wounding, irradiating and drying was the most consistently satisfactory method for producing the quantity

of spores required in inoculation tests on the foliage of greenhouse-raised potatoes and tomatoes. Cultures were grown for 10 days at 26 degrees C. on potato dextrose agar, then the aerial hyphae were wounded by scraping the surface of the culture with a safety razor blade. The wounded cultures were next exposed at a distance of 10 cm. to an ultraviolet light (2350 Å) for 1 minute, and were dried for 16 hours at room temperature with the petri plate cover in a raised position. Many conidiophores and spores in varying stages of development were visible on microscopic examination at the expiration of this period. The spores were mature and ready for harvest two days after irradiation.

The disease and its physiology were studied mostly in the greenhouse. Tomato plants were grown in a greenhouse having an approximate temperature range of 24° to 29° C. Three tomato plants per 4-inch pot were used in many tests because of the space limitations of the incubation chambers. Crowding increased susceptibility: for example, the magnitude of infection as measured by the percentage of the foliage area diseased was increased from 13 per cent for single plants to 33 per cent for ten tomato plants per pot. However, results were comparable in tests that were duplicated with one and with three plants per pot. Plants 6-8 weeks old and in the 5-7 leaf stage were inoculated with 20 ml. per pot of a spore suspension containing approximately 25,000 spores per ml. Inoculum was prepared from cultures treated with the wound-irradiate-dry technique previously outlined. The plants were maintained in a moist chamber for 36 to 48 hours at 100 per cent humidity. Incipient infections were visible after this period as minute necrotic spots surrounded by a chlorotic halo.

Most of the disease tests were made on tomatoes, since large numbers of uniform plants can be grown readily in the greenhouse. However, many tests were duplicated on Irish Cobbler potatoes, not only to determine disease reaction on this host but also to ascertain the degree of universality of the phenomena under study. The plants were grown and inoculated at a temperature of 18° to 24° C. This temperature was below the optimum for disease development, but it was the most satisfactory for tests with potato plants, as higher temperatures had adverse effects on the host.

Measurement of the severity of early blight on the test plants must include the number and size of lesions and their effect on the host tissue. Counts of the number of disease spots per unit does not indicate the complete host reaction to the disease (i.e. to the established pathogen) but rather the host's resistance to infection or invasion. The wide variation in the disease reaction of the upper and lower leaves would be indicated by the mean diseased area for these tissues. To be quantitative, such a process would require counting

the number of diseased spots and measuring their area, which is far too laborious to be practicable on a large number of plants. Estimates of the amount of host tissue showing disease symptoms were therefore used as a measure of disease intensity. The method of Horsfall and Heuberger (10) was modified by using the amount of leaf area having diseased symptoms. Five disease categories were arbitrarily selected as follows:

<u>Grade</u>		<u>Amount of leaf area diseased</u>
0	—	No disease evident
1	—	Trace to 25 per cent of leaf area diseased
2	—	26 to 50 per cent of leaf area diseased
3	—	51 to 75 per cent of leaf area diseased
4	—	76 to 100 per cent of leaf area diseased

Each leaf of the test plants was graded and assigned the appropriate number. The category numerals recorded for all the leaves in a treatment were totaled. The disease index was calculated for each treatment by the formula:

$$\text{Disease index} = \left\{ \frac{\text{sum of leaf category numbers}}{\text{no. of leaves} \times 4} \right\} 100$$

(% foliage area diseased)

The disease index so obtained is a relative measure of the percentage of foliage area affected by the pathogen.

EXPERIMENTAL RESULTS

A. Physiologic variation of *Alternaria dauci* f. *solani*

The existence of physiologic races differing in (a) the amount of spore production, (b) the rate of growth, (c) the formation of substrate pigment, (d) the color, texture and other characteristics of the mycelium in culture, (e) the frequency of mutation, (f) the degree of pathogenicity, and (g) the size of the spores have been demonstrated by Bonde (4), Pitman (17), Klaus (11) and Neergaard (16). The monoconidial isolates utilized in the present study were therefore examined for the range in variation in some of these characters and their relation to pathogenicity.

Cultural Characters

Preliminary differentiation of physiologic races was accomplished by culturing the single-spored isolates on potato dextrose and Smith-Humfeld agar. Each isolate was inoculated in triplicate onto each of

the two nutrient media contained in flasks (250 ml. flasks containing 30 ml. of media). The flasks were incubated at 26° C. for 14 days, then notes were taken on mycelial texture, surface profile, mycelial color, substrate color and diameter of growth. Mycelial colors were based on Ridgeway's (21) standards. The exact color of the substrate pigment varied for the same race in different trials and this character was recorded as by Bonde (4) as chromogenic, intermediate (variable or faint production of pigment) and nonchromogenic. The results with 16 distinctive isolates on potato dextrose agar are summarized in Table 2. These cultural characters were found to be constant in comparisons at 6 months, 1 and 2 years after the original trial. Therefore, these isolates are designated as races (see Figure 1).

TABLE 2. Cultural characteristics on potato dextrose agar of 16 monoconidial isolates of *Alternaria dauci* f. *solani*.

Isolate number	Mycelial texture	Surface profile	Mycelial color	Substrate color*	Av. Dia. growth 14 days
1B1	Cotton	Thickly tufted	Mouse gray	C	3.2 cm.
1B4	Felt	Smooth	Center — pale vinaceous pink. Rim — blackish mouse gray	C	3.4
1B5	Felt	Smooth	Light mouse gray	C	4.8
1C1	Felt	Smooth	Carbon gray	N	8.6
4A2	Felt	Smooth	Flesh pink	C	3.8
4A4	Felt	Smooth	White	I	4.4
5A1	Cobweb	Smooth	Center — white. Rim — blackish mouse gray	I	9.0
5A3	Cobweb	Smooth	Center—pale grayish vinaceous pink. Rim—blackish gray	C	7.5
8B1	Cotton	Frayed	Neutral gray	C	9.0
13D1	Cotton	Frayed	Mouse gray	C	9.0
16A1	Cotton	Frayed	Neutral gray	I	6.8
17A1	Cotton	Rough	Light mouse gray	C	8.9
19B1	Cobweb	Frayed	Neutral gray	C	8.2
22A1	Cotton	Rough	Center — light mouse gray. Rim — mouse gray	C	8.2
23A1	Cotton	Frayed	Mouse gray	C	8.3
24A1	Cotton	Rough	Deep olive gray	C	8.1

*C—chromogenic, I—intermediate, and N—nonchromogenic.

Sporulation

The degree of sporulation of the different races was determined by using the scrape-irradiate-dry technique. Triplicate petri plates of all races were grown for 10 days in the dark under controlled temperatures, treated for sporulation and examined with a microscope for spores 2 and 4 days after treatment. A range in spore production

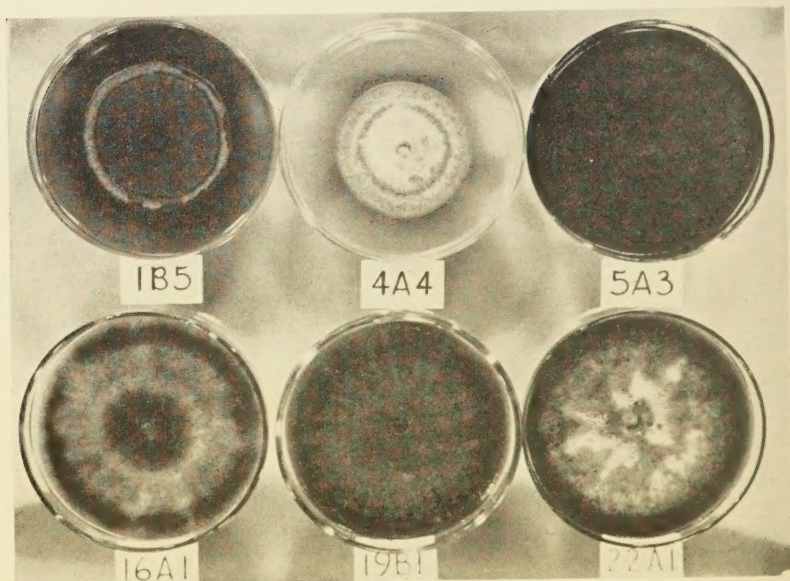


FIGURE 1. Six races of *Alternaria dauci* f. *solani* on potato dextrose agar.

from 0 to as many as 10,000,000 per plate was found among the races. The plates were rated arbitrarily on microscopic examination to compare the wide variation in this character. The classes were as follows:

<u>Class</u>	<u>Amount of sporulation</u>
0	No spores were found on a thorough examination of all the plates.
Trace	Fewer than 10 spores were observed on all the plates.
Sparse	Spores were readily found on each plate, but less than 10,000 per plate.
Abundant	10,000 or more spores produced per plate.

The results of three trials at intervals of approximately one year are recorded in Table 3.

TABLE 3. Relative sporulation of 13 races of *Alternaria dauci* f. *solani* during a 3-year period.

<i>Race number</i>	<i>Relative degree of sporulation on</i>		
	<i>April 1946</i>	<i>March 1947</i>	<i>November 1948</i>
1B1	Abundant	Sparse	Sparse
1B4	Sparse	0	0
1B5	Abundant	Abundant	0
1C1	Sparse	Trace	0
4A2	Sparse	Sparse	0
4A4	Sparse	Sparse	0
5A1	Abundant	Sparse	Trace
5A3	Trace	0	0
8B1	Abundant	Abundant	Sparse
13D1	—	Abundant	0
16A1	—	Abundant	0
17A1	—	Abundant	0
19B1	—	Abundant	Abundant

There are distinct differences between races in the degree and regularity of sporulation. Both types of variation are readily illustrated by races 1B1, 1B4, and 1B5 which were monoconidial isolates from the same parental culture and had identical cultural histories. Race 1B1 sporulated abundantly in the early trials and poorly in later tests. Race 1B5 also sporulated profusely in the first two trials but suddenly lost this character in the second year. The race 1B4 sporulated only sparsely in the first trials and then failed entirely to sporulate. Race 8B1 consistently produced abundant spores for a longer time than any other tested over the two-year period.

Pathogenicity

Variation in the degree of sporulation of different races of *Alternaria dauci* f. *solani* prevents the preparation of equal inocula for their comparison in foliage infection trials. Other investigators have circumvented this difficulty by devising techniques to determine the virulence and the host range of their physiologic races on specific plant organs (4, 11, 16, 19 and 22). In the present study three methods of determining comparative virulence on John Baer tomatoes were investigated: (a) inoculation of the foliage of young plants in moist chambers with spore and mycelial fragments, (b) inoculation of stems with mycelium, and (c) the inoculation of sterile seedlings raised in test tubes.

The races were compared for differences in foliage infection on greenhouse-raised tomatoes in the 5-7 leaf stage of growth. Inoculum was prepared from 10-day-old cultures by the scrape-irradiate-dry technique. The relative sporulation between these races after 48 hours ranged from 0 to abundant; therefore, inoculum was prepared from the entire colony of each race by maceration (with 100 ml. of water) for 1 minute in a Waring blender. These suspensions were atomized onto the foliage of the test plants. Nine plants for each race were inoculated and maintained for 48 hours in separate humidity chambers. The plants were rated for disease 6 days after inoculation, by estimating the percentage of foliage area affected, as outlined under Materials and Methods. For convenience of comparison to the other methods, however, the data have been converted as follows: 0 indicates no infection; slight, less than 5 per cent; moderate, 5 to 25 per cent; and severe, more than 25 per cent of the foliage area affected by the disease.

TABLE 4. Relative virulence of 12 races of *Alternaria dauci* f. *solani* as determined with three different infection techniques on John Baer tomato.

Race number	Relative virulence		
	Seedlings	Foliage	Stems
1B1	Slight	Slight	Slight
1B4	Moderate	—	Moderate
1B5	Slight	Slight	0
1C1	Slight	Slight	Moderate
4A2	Moderate	Moderate	—
4A4	0	Slight	Slight
5A1	Slight	Moderate	0
5A3	Slight	0	0
8B1	Severe	Severe	Moderate
13D1	Moderate	Severe	Moderate
16A1	Severe	Moderate	—
17A1	Severe	Severe	—

The data for a typical foliage infection trial are listed in Table 4. The sporulative data listed in Table 3 for March 1947 were recorded from the cultures used to inoculate these plants. These data indicate that the virulence is independent of the number of spores produced by the race. None of the poorly sporulating isolates had a severe disease rating. However, two poorly sporulating races, 1B4 and 4A2, were classed as moderately virulent. Conversely, 1B5, which sporulated abundantly, had but slight virulence.

Stem infection by *A. dauci* f. *solani* at the ground line on young tomato plants produces a canker, first described by Rosenbaum (22) as foot-rot. The relative virulence of the various races on tomato was also determined on this organ. Uniform-sized pieces of inocula, cut with a quarter-inch cork borer from 10-day-old cultures, were placed with the aerial surface adjacent to the stem. The inoculated area was covered with moist cotton which was fastened around the stem. Stems of three plants were inoculated with each race 2 and 6 inches above the soil line. The cotton was moistened twice daily and removed 10 days after inoculation. At that time, infected areas of varying sizes had developed and the infection was graded as "severe" if the canker completely girdled the stem, "moderate" for cankers more than 1 centimeter long but not girdling the plant, "slight" for cankers less than 1 centimeter long, and as a "trace" where small necrotic flecking occurred under the inoculum.

Table 4 gives the results for a test in which the stem was wounded by scraping the surface lightly with a scalpel. Differences or variability in pathogenicity of the different races determined in this way agreed in general with the results from foliage infection. In tests where uninjured stems were inoculated, a much lower disease index was obtained, that is, only the more virulent strains produced infection.

The most sensitive measure of pathogenicity was found to be the infection of seedlings grown aseptically. Essentially the method of Neergaard (16) was used in these laboratory tests, except that water agar was substituted for moist filter paper as a substrate. Seeds were surface sterilized in a 1-1000 mercuric chloride solution for 1 minute and washed thoroughly in sterile water. Five seeds were imbedded in 15 ml. of water agar in 2 x 15 cm. test tubes and germinated at room temperature. Uniform seedlings were selected after germination and inoculated by inserting discs cut from young cultures of the test races grown on potato-dextrose agar. Each race was tested against an average of 20 plants in a single trial. Disease development was observed daily. The data in Table 4 were recorded 10 days after inoculation. The relative degree of disease development was recorded by the scale given below.

<u>Grade</u>		<u>Disease development</u>
0	—	none
1	—	slight (necrotic flecks around stem)
2	—	moderate (extensive necrosis along stem)
3	—	severe (host plant killed)

The disease index was obtained from the average for all seedlings in a given isolate-host test. The mean index has been converted to its general categories of 0, slight, moderate or severe for comparison in the tables. The relative virulence recorded by this technique agree with that obtained by foliage infection.

Comparisons of ten races of *A. dauci* f. *solani* on four species of *Lycopersicon* further demonstrated the range in virulence that exists in this fungus. The four host species, *Lycopersicon esculentum* var. John Baer, *L. pimpinellifolium* (U.S.D.A. 41W72), *L. peruvianum*, and *L. hirsutum* (Grown from cuttings supplied by Dr. T. M. Currence of the Division of Horticulture, University of Minnesota, St. Paul, Minnesota.) were grown to the 6-8 leaf stage in 4-inch pots. Four plants of each species were inoculated with a spore and mycelial suspension of the races and incubated in a moist chamber for 48 hours. Plants were rated for disease development five days after inoculation and the data converted as in previous trials for the comparison of virulence of races. The data are presented in Table 5. The selection of *L. pimpinellifolium* tested was the most susceptible of the four species; *L. esculentum* was second; *L. peruvianum* was third; and *L. hirsutum* was the least susceptible. The virulence of the races of *A. dauci* f. *solani* tried was not specific for the hosts inoculated and the more virulent the strain, the greater the degree of disease development on each of the host species.

TABLE 5. Comparative disease reaction resulting from inoculating four species of *Lycopersicon* with ten races of *Alternaria dauci* f. *solani*.

Race number	Disease reaction of <i>Lycopersicon</i> species			
	<i>L. pimpinellifolium</i>	<i>L. esculentum</i>	<i>L. peruvianum</i>	<i>L. hirsutum</i>
1B5	Slight	Slight	0	0
1C1	Slight	Slight	0	0
4A2	Moderate	Moderate	Slight	0
4A4	Slight	Slight	0	0
5A1	Moderate	Moderate	Slight	0
5A3	0	0	0	0
8B1	Severe	Severe	Severe	Slight
13D1	Severe	Severe	Moderate	0
16A1	Severe	Moderate	Moderate	0
17A1	Severe	Severe	Severe	Slight

Instability of pathogenic and sporulative characters of physiologic strains

Maintenance of *Alternaria dauci* f. *solani* in culture over a period of time results in marked changes in sporulation and pathogenicity. This is illustrated in Table 3, which records the changes in sporulation of the races during a 3-year period. The changes may be slow, as in race SB1, or rapid, as with race 17A1. The latter was isolated in January 1947 and sporulated actively in all tests until August of that year, when it suddenly ceased to produce conidia. Many subsequent attempts to induce sporulation of this strain were totally unsuccessful. Furthermore, the change in sporulative capacity does not appear to be accompanied by any visible change in cultural characters, as these were compared frequently with the original observations. No races or sectors were found in this study in which the sporulative capacity was increased.

The virulence of the various races was also found to be unstable. All of the studies reported under pathogenic variation were completed and duplicated with similar results within a 6-month interval in late 1946 and early 1947. At that time (Tables 4 and 5) only the most recently isolated races (SB1, 13D1, 16A1, and 17A1) were highly virulent. Repeated comparisons of the virulence of these races in 1948 demonstrated SB1 as moderately pathogenic and all the remaining races produced only a trace or less of disease on the test seedlings.

The instability of these two physiologic characters has been demonstrated by Neergaard (16) to occur in all three pathogenic forms of *A. dauci*. He also found a sector from an isolate of *A. dauci* f. *porri* which sporulated profusely and spontaneously. Such inconsistency in cultures complicates a thorough investigation of pathogenic variation among strains.

B. Factors affecting the interaction between host and pathogen

Age of foliar tissue

Early blight of potatoes and tomatoes is frequently alluded to as a disease of senescent or weakened plants. Furthermore, it has been generally observed to attack most virulently the lowermost and, therefore, the oldest leaves. This is readily demonstrated by the inoculation of the foliage of greenhouse-raised plants. Symptoms are visible, under optimum conditions, on the lower leaves 48 hours after inoculation as small necrotic spots surrounded by a narrow, faintly chlorotic ring. Subsequent disease development is rapid on these leaves, and the oldest may wilt, and fall from the plant 4 to 6 days after inoculation. Minute examination of all the individual leaves on the plant at this time reveals a good proportion of the first two

leaves at the top of the plant as symptomless, with the remainder having minute necrotic flecks less than 1 mm. in diameter. Descending to older leaves down the plant, progressively more severe symptoms are found as evidenced by more necrosis and chlorosis of the leaflets and with epinasty of the petiole. The lowermost leaves are completely wilted and dead (see Figures 2 and 3).



FIGURE 2. John Baer tomato plants five days after inoculation with a virulent race of *Alternaria dauci* f. *solani* showing the progressive increase in the severity of the disease from the topmost and youngest leaves to the lowermost and oldest leaves.

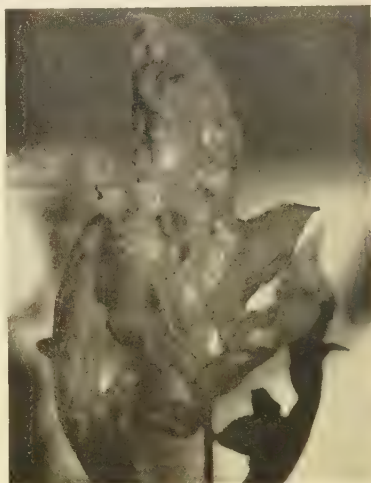


FIGURE 3. Mature leaflet of John Baer tomato five days after inoculation with a virulent race of *Alternaria dauci* f. *solani* showing the severe development of disease lesions that precedes the complete collapse and defoliation of the leaf.

Similar symptoms of epinasty, chlorosis, and necrosis were produced within 24 hours on young tomato plants when the stems were immersed in sterile culture filtrates from *A. dauci* f. *solani*. Filtrates from pathogenic (17A1 and SB1) and non-pathogenic (4A4) races were tested and found to be equally toxic. Pound and Stahman (18) have recently reported duplication of some early blight symptoms by toxic substances produced by the fungus. Resistance in young leaves to such fungus toxins would explain in part the reduced disease development in such tissue. However, no differences in degree of response were found between young and old leaves of plants immersed in the toxic culture filtrates.

Many of the topmost, apparently disease-free leaves were found to harbor the pathogen without visible symptoms. Leaflets representative of the various disease types were collected and surface sterilized

in 0.1 per cent mercuric bichloride solution for 2 minutes, washed in a dilute solution of sodium hypochlorite, and placed individually in sterile petri plates. A thin layer of cooled potato dextrose agar was poured over these leaflets. Those from the older leaves of the plants, which showed typical early blight lesions 4 to 8 mm. in diameter, yielded 100 per cent pure cultures of *Alternaria dauci* f. *solan*i. The fungus was reisolated from 70 per cent of younger leaflets, in which infection was visible as minute necrotic flecks. In both of these groups, the fungus originated from the necrotic area in the leaflet. The organism was also obtained in pure culture from 30 per cent of the symptomless young leaves. Control leaflets which had been sprayed with the inoculum and allowed to dry immediately under conditions unfavorable to infection did not yield the fungus. McCallan and Wellman (13) have reported that fewer infection lesions per unit area are found on the youngest leaves. The observations reported here indicate that infections are present, but fail to develop sufficiently to be easily detected in very young tissue. Such symptomless infections indicate that the apparent immunity of young tissue is not due to failure of the infective hyphae to penetrate but rather to some physiological mechanism that inhibits subsequent development.

Light intensity

The severity of early blight on the foliage of young tomato and potato plants was found to be markedly increased by shading from direct sunlight. Greenhouse-grown plants were uniformly inoculated and incubated, then placed in shade or direct sunlight. The shade was provided by screens arranged so as to exclude direct sunlight, with exposure to only north light and with provision for free air circulation around the plants.

TABLE 6. The effect of shading on the development of early blight on the foliage of Irish Cobbler potato plants.

<i>Treatment</i>	<i>Per cent of leaves infected</i>	<i>Per cent of foliage area diseased</i>	<i>Per cent of stem area diseased</i>
Sunlight	70.6	48.3	28.1
Shade	80.5	70.5	56.3

The data in Table 6 illustrate disease development on Irish Cobbler potato foliage in the two environments. Disease was greater on the shaded plants, as measured by the percentages of the leaves showing disease symptoms and of the foliage and stem areas diseased. These increases in disease ratings were not due to chlorosis and abscission of the leaves from the plants under lower light intensities because such symptoms did not develop on noninoculated control plants kept

in this environment for the duration of the experiment. Relative humidity was the same for both locations throughout the experiment, as shown by hygrothermograph records. Temperature variation was greatest during sunlight hours, with a maximum reading of 4 to 6 degrees higher at noon in the nonshaded area. The mean hourly temperatures were 78 and 80 F. respectively for the shaded and unshaded areas. It seems improbable that this temperature difference would account for the differences in disease development. Similar results for the effect of light intensity were observed in the development of early blight on young tomato plants (see (Figure 4).



FIGURE 4. The effect of shading on early blight development on young tomato plants (var. Comet). A. Sunlighted control. B. Post-inoculation shading.

Preinoculation exposure of healthy plants to diffuse light had no detectable effect on the severity of disease. The comparison of disease development on young tomato plants exposed to low light intensities before and after inoculations is given in Table 7. Shade-preconditioned plants were maintained in diffuse light in the greenhouse for 2 days prior to inoculation. Direct sunlight did not penetrate the infection chamber, so the 2 days of inoculation made a combined period of 4 days of low light intensities prior to the development of disease symptoms. Disease notes were recorded 4 days after inoculation, therefore, the post-inoculation-shaded plants were exposed to

TABLE 7. The effect of pre- and post-inoculation shading on the development of early blight on foliage of John Baer tomato plants.

<i>Treatment</i>	<i>Per cent of leaves infected</i>	<i>Per cent of foliage areas diseased</i>
Sunlight	37.1	22.2
Pre-inoculation shading	34.2	17.6
Post-inoculation shading	69.1	38.2

low light intensities for an equivalent period of time. There was little difference in the degree of disease development between the preinoculation-shaded plants and those exposed to normal sunlight, but those plants shaded after removal from the infection chamber were more severely attacked.

Tests with detached leaflets substantiated the effect of light on disease development. Greenhouse-raised Irish Cobbler potato and John Baer tomato plants were placed in shade and in sunlight in the greenhouse 48 hours prior to inoculation. Leaflets from the lowermost three healthy leaves of each plant were collected at the end of this period to supply tissues of approximately the same disease susceptibility. These leaflets were placed with the upper surface exposed on sterile water in sterile petri plates. Leaflets from the shaded and sunlit plants of tomato and potato were divided equally into shaded and sunlit environments in the petri plates so that ten leaflets represented each host in the pre- and post-inoculation environment combinations. The leaflets were inoculated by atomizing a spore suspension onto the upper surface. Disease symptoms appeared slowly on detached leaflets. Tomato leaflets exposed to sunlight after inoculation showed no visible signs of infection during the experiment, regardless of the pre-inoculation amount of light.

Post-inoculation shading, however, resulted in 100 per cent infection of the tomato leaflets, and in some instances one-third to one-half of the leaf tissue was killed by the pathogen. Disease development was more severe on the potato than on the tomato leaves. Diseased spots and chlorosis occurred on all the sunlit potato leaflets. The shaded leaves were more severely attacked, all leaflets being killed within 13 days after inoculation. Again, no difference was noted in the susceptibility to disease of leaflets from the pre-inoculation shaded and sunlit plants.

The combined effect of light and leaf position on disease development is illustrated by an experiment with Irish Cobbler potatoes. In this test the magnitude of infection was 33.4 per cent of the foliage area affected for the plants under normal light conditions, as compared to 50.7 per cent affected foliage area for the shaded plants. The leaves were graded individually from a total of 117 shoots for the

lighted and 106 shoots for the shaded plants. The average amounts of foliage area affected for the two treatments are compared in Figure 5. The topmost, fully-opened leaves (no. 1) of the sunlit plants show a marked difference in the area affected by disease over those succes-

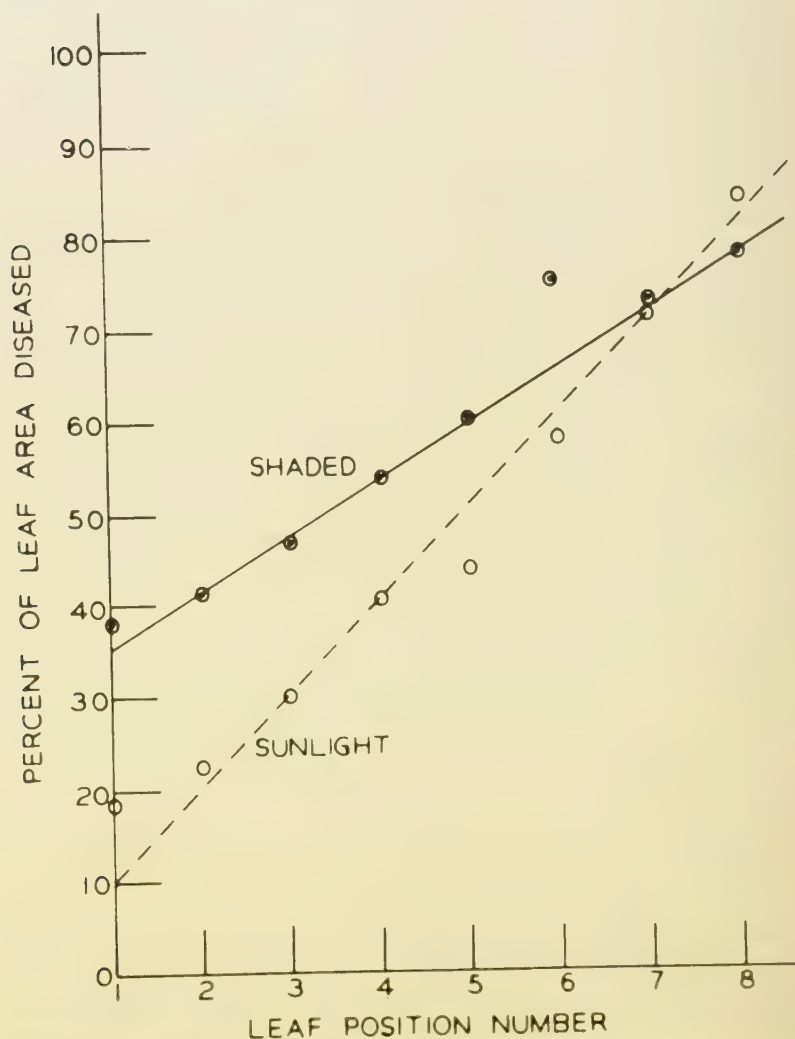


FIGURE 5. Relation of leaf position (designating the top leaf number 1) on shaded and sunlit potato plants to percentage of foliar area diseased.

sively of the lower and older ones. The relationship closely approaches a straight line with a fairly steep slope. The same relationship in amount of disease is shown by the leaves on the shaded plants, i.e., the amount of diseased area increased with maturity and lower position on the plant. Here, however, the differences between successive leaves are less and a more gradual slope results.

The amount of leaf area affected by the disease on the younger leaves of the shaded plants is greater than those in the sunlight by approximately 20 per cent. The older leaves, however, have a greater susceptibility and the degree of disease for both environments becomes equal for the oldest leaves. Hence the increased disease development under low light intensities appears to be largely due to lowering of resistance in young tissues of the host. Apparently this defensive mechanism has already disappeared in old tissues during the processes of aging.

Foliar pruning

The resistance of the older leaves in the lower positions on the young plants can be increased when young growth is suppressed by the pruning of growing points and young leaves. This was illustrated by tests such as the one recorded in Table 8. Greenhouse-grown John

TABLE 8. Effect of foliar pruning on the development of early blight on the foliage of John Baer tomato plants.

<i>Treatment</i>	<i>Per cent of leaves infected</i>	<i>Per cent of foliage area diseased</i>
Control plants		
Young foliage (top 5 leaves)	10.0	2.5
Mature foliage (lower 5 leaves)	80.0	59.9
Young foliage (Mature leaves pruned)	7.7	3.8
Mature foliage (Young growth pruned)	30.0	14.3

Baer tomato plants were divided into three treatments, replicated six times, 15 days prior to inoculation. In one set, designated as "mature foliage", all the growing points and the youngest leaves were removed, the five oldest leaves remaining on each plant. A second set, representing "young foliage", was prepared by removing the lowest and oldest leaves from each plant and allowing five young leaves to continue to grow and develop on the top of the plant. The last group was maintained as control plants that were allowed to develop in a normal manner. The plants were inoculated as previously outlined. Notes on diseased area were recorded for individual

leaves. The data for the control plants, however, were calculated separately for the five topmost and five lowermost leaves for comparison with the corresponding leaves of the pretreated plants bearing young and mature foliage.

The mature foliage of the plants on which young growth was suppressed was much more resistant to disease attack than the mature leaves of the control plants. However, the disease development in this mature foliage was greater than in the young foliage of both the control and the mature-leaf defoliated plants. Suppression of growth on young plants appears to decrease the susceptibility of the mature leaves but never to the degree of that in the young, growing tissue.

Crop maturation and sugar content of leaves

The effect of sunlight on the development of early blight on young plants suggested a correlation between photosynthetic carbohydrate products in the leaf tissue and the susceptibility of that tissue to disease. The changes of the sugars with maturation of field-grown tomatoes were studied with the coincidental disease development to determine possible biochemical relationships.

Plants from a tomato (var. Comet) field plot, to which no fungicides were applied, were used for analyses. Samples were collected on clear, cloudless days from ten random plants for each series of determinations. The morning samples were taken at 9 a.m. and the afternoon samples were gathered at high solar noon to minimize the diurnal effect on sugar content for tomatoes demonstrated by Went (27). Samples of young, disease resistant tissue were collected from the three topmost, fully-opened leaves and of bottom older leaves from green, fully matured leaves at the base of the vines. The tissue extract was prepared by freezing the sample with carbon dioxide snow and removing the juice by pressure after the sample thawed, then clarified according to the methods outlined by Schlenker (23). Sugars were determined colorimetrically by the alkaline copper-reagent method of Somogyi (24). The reducing and non-reducing sugars were calculated on the basis of a glucose and sucrose standard curve, respectively. The sugar values were corrected for the non-sugar-reducing substances and converted to milligram per cent of fresh weight by the methods of Schlenker (23). The data for three dates are presented in Table 9.

More reducing sugars were found in the top leaves than in the lower leaves, and those sugars also showed a tendency to increase in the tissues as the plants aged; but disease development was not correlated with the content of reducing sugars. The bottom leaves were severely attacked when sugar content was relatively low, while the severest attack on top young leaves occurred when the concentrations

TABLE 9. Soluble carbohydrate changes and disease development accompanying the maturation of tomato plants in the field, sampled on three different dates.

Sample	August 14		August 22		September 5	
	9 a.m.	1 p.m.	9 a.m.	1 p.m.	9 a.m.	1 p.m.
Top leaves						
Reducing sugars*	27.7	—	29.4	31.5	36.7	56.1
Non-reducing sugars**	6.3	—	6.2	11.7	0	0
Percent leaves infected	0	—	Trace		100	
Bottom leaves						
Reducing sugars*	10.7	—	10.9	10.7	17.4	17.5
Non-reducing sugars**	4.3	—	3.2	6.8	0	0
Percent leaves infected	Trace	—	35		100	

*Reducing sugars determined as glucose and expressed as miligram per cent of fresh weight.

**Non-reducing sugars determined as sucrose and expressed as milligram per cent of fresh weight.

of these sugars had doubled. The non-reducing sugar content appears more closely correlated with disease incidence. The bottom leaves contained less non-reducing sugars and had a higher incidence of disease than the top leaves, and these components had completely disappeared from both tissue samples when 100 per cent of the leaves were attacked.

Fungicidal and hormonal chemicals

The control of early blight of potatoes and tomatoes with fungicides had never been markedly successful until the appearance of some of the new carbamate complexes. The Rhode Island spray trial for the 1947 National Cooperative Potato Spray Fungicide Experiment (7) revealed the wide variation in effectiveness of materials for the control of this disease. Unfortunately, the unsprayed control plants in this test had been completely defoliated by late blight, caused by *Phytophthora infestans*, when early blight became epiphytotic. However, with the exception of Zerlate, the six materials listed in Table 10 had all given approximately the same degree of control of defoliation by late blight by mid-August, and essentially equal amounts of foliage were found in the different treatments.

Notes were taken on the percentage of the green foliage area affected by early blight disease, according to the grading system of Horsfall and Barratt (9). The marked increase in the disease in the Phygon-sprayed plots over the remaining materials suggested an effect on the defensive mechanisms of the host. The two formulated products, Parzate (65 per cent zinc ethylene bis dithiocarbamate), and Phygon (87 per cent 2,3 dichloro-1,4 naphthoquinone), which showed the extremes in disease control, were selected for study in the laboratory and greenhouse. Dosages were based on the active

TABLE 10. Control of early blight by various fungicides on Green Mountain potatoes in the field.

Treatment	Dosage per 100 gal.	Per cent of foliage area infected with early blight		Per cent defoliation	
		Aug. 13	Aug. 28	Aug. 13	Aug. 28
Control	—	—	—	93.2*	100.0**
Parzate	2 lbs.	7.7	10.6	10.2	17.7
Dithane D-14	2-2-1	14.7	30.1	17.3	48.3
+ ZnSO ₄ +lime					
Bordeaux mixture	8-4-100	10.2	41.2	20.0	34.2
Zerlate	2	11.0	53.3	37.3	77.3
Tenn. Tribasic copper	4	21.7	60.2	14.5	42.3
Phygon	½	30.5	90.7	6.8	57.2

*Defoliation from late blight caused by *Phytophthora infestans*.

**Defoliation from both late and early blights.

component. Sodium 2,4-dichlorophenoxyacetate (designated hereafter as 2,4-D) was included as a material known to have marked effects on the carbohydrate metabolism of herbaceous plants (6, 14, 20).

The three materials were compared for fungitoxicity to spores of *A. dauci* f. *solani* by the standard spore-germination test of the American Phytopathological Society (2). The laboratory assay revealed that the two fungicides had approximately the same degree of toxicity to the fungus. Phygon had an LD 50 of 4.7 and LD 86 of 7.1; Parzate had LD 50 of 4.7 and LD 86 of 11.0, and 2,4-D was nontoxic to the spores of this fungus in dosages up to 100 p.p.m. The slope of the two fungicides crossed at LD 50; Phygon having the steeper slope. Therefore, the two materials have approximately equal fungicidal potentials for this pathogen.

Greenhouse-grown young tomato plants were treated with these chemicals to determine possible effects on the host's natural resistance. The fungitoxic properties were minimized by two experimental methods. In the first and most effective method, 4-inch pots of the young plants were irrigated with 50 ml. of the test solution 1 day prior to inoculation. The plants were inoculated and rated for disease in the usual manner. Unfortunately, this method exposes material to reaction with the components of the soil. The second method employed post-inoculation sprays which eliminated this variable. The plants were inoculated and held in the infection chamber for 48 hours. The foliage was sprayed daily with the test solution after removal from the chamber. Preliminary tests demonstrated little measurable effect from single applications of the solutions presumably because of insufficient absorption of the materials by the foliage.

The most conclusive data were obtained with the soil-drench method. Distinct increases in disease development over the control

series which were similar in magnitude to that caused by shading were obtained with dosages of 1:5,000,000 for 2,4-D and 1:5,000 for Phygon. Similar changes in disease reaction were produced by daily spraying of infected plants with Phygon and 2,4-D (see Tables 11 and 12). The 1:500,000 drench of 2,4-D caused distortion of the young leaves on the plants and this may have been accompanied by further abnormal physiological changes that further altered the disease reaction. The lower concentration of Phygon had no appreciable effect on the amount of disease and probably was too dilute to affect the host's physiology. The dosages of Parzate tested had no consistent effect on disease development.

TABLE 11. Effect of sodium salt of 2,4-D, Phygon, and Parzate applied as pre-inoculation soil drenches on the susceptibility of young tomato plants to *Alternaria dauci* f. *solani*.

Treatment	Concentration of drench	Per cent foliage area affected by disease			
		Trial no.			
		I	II	III	IV
Control	—	15.3	58.2	60.1	30.2
Shade	—	31.2	70.5	75.3	53.3
2,4-D	1:500,000	25.4	56.8	64.5	—
2,4-D	1:5,000,000	35.7	74.0	73.3	48.4
Phygon	1:5,000	31.1	72.3	72.8	50.9
Phygon	1:50,000	12.2	60.5	63.5	—
Parzate	1:1,000	13.1	61.1	—	37.7
Parzate	1:10,000	4.9	53.9	—	—

TABLE 12. Effect of sodium salt of 2,4-D, Phygon and Parzate applied as post-inoculation sprays on the susceptibility of young tomato plants to *Alternaria dauci* f. *solani*.

Treatment	Concentration of spray	Per cent foliage area affected by disease	
		Trial I Trial II	
Control	—	45.9	39.1
2,4-D	1:50,000	70.1	62.8
Phygon	1:1,000	62.1	50.0
Parzate	1:1,000	49.1	36.6

C. Metabolic responses of *Alternaria dauci* f. *solani* to extracts from young resistant and old susceptible tomato leaf tissues

Changes in disease reaction of tomato and potato foliage induced by different conditioning agents suggest that the resistance of the top leaves of the hosts is of a physiological nature. Furthermore, the successful establishment of infection in young tissue under normal conditions and the subsequent suppression of disease development

until the tissue matures indicates that disease development in such young tissue was not prevented by morphological defensive mechanisms. Therefore, tissue extracts were studied to determine possible relations between cellular contents and disease reaction.

The growth of *Alternaria dauci* f. *solani* in extracts from young and mature leaves indicated a difference in the two tissues. In a typical test, the three topmost fully opened leaves for young tissue and the three lowermost healthy leaves for mature tissue were collected from greenhouse-raised John Baer tomato plants and the cell sap was expressed from each sample with a Carver press. The extracts were diluted with an equal volume of distilled water and the proteins were removed by filtration after heating in a water-bath at 100° C. for ten minutes. The filtrate was divided into 25 ml. aliquots in 125 ml. flasks and these were sterilized by autoclaving. The flasks were inoculated with race 5A1 and incubated for 11 days at 26° C. The dry weights of the mycelial mats were determined and an average mycelial weight of 190 and 155 mgs. was obtained respectively for the mature and the young tissue extracts. A similar difference in the amount of mycelial growth was also found in extracts of the 2 groups of leaves that were sterilized by a Seitz filter. However, this technique was limited by the difficulty of collecting sufficiently large volumes of the cell extracts for the comparison of races of different pathogenicity and for determination of constituents affecting the pathogen.

The principal sugars, glucose and sucrose, of tomato foliage were equally utilized for growth and respiration by the pathogen. Growth studies of a virulent (8B1) and an avirulent (4A4) race on different quantities of sucrose and glucose based on equivalent amounts of carbon showed that the amounts of growth at low concentrations were similar, and that at high concentrations, sucrose was more readily utilized, (see Table 13). Respirometric studies of glucose and sucrose gave respectively 46 to 49 per cent increases over the CO₂ of endogenous respiration and indicate the equal utilization of these sugars for aerobic respiration.

TABLE 13. Growth of a virulent (8B1) and an avirulent (4A4) race on media containing sucrose and glucose of equivalent carbon content.

Sugar	Molar conc.	Amount carbon grams/liter	Weight of mycelial mat	
			4A4	8B1
Sucrose	0.057	0.84	43 mg.	44 mg.
Sucrose	0.293	4.21	66	105
Glucose	0.114	0.84	46	49
Glucose	0.586	4.21	55	84

DISCUSSION

The pathogenicity of *Alternaria dauci* f. *solani* in early blight, the defoliation disease of tomato and potato, is determined by the virulence of the pathogen and the resistance of the host. That *Alternaria dauci* f. *solani* comprises a number of physiologic races as demonstrated by Bonde (3, 4) and others (14, 24, and 22) was confirmed in the present study. The range in variation of cultural and certain physiologic characters was determined for a number of isolates from material collected in Minnesota and Rhode Island. Distinct races were found which differed in cultural characters, in sporulation and in degree of virulence. However, all races had the common characteristic of being weakly pathogenic on young foliar tissue. The relative degree of pathogenicity of different races was essentially similar when compared in virulence on young seedlings, foliage and stems of tomato.

Two types of resistance, permanent and temporary, to *Alternaria dauci* f. *solani* exist in solanaceous hosts. Permanent resistance is governed by genetic factors in the host as illustrated by the disease reaction of four *Lycopersicon* spp. to different pathogenic races. For example, *L. hirsutum* consistently had the least and *L. pimpinellifolium* the most disease in all comparative inoculation tests.

Temporary resistance occurs in young tissues and is dependent on physiological factors in the host. Such resistance is affected by the age of the foliar tissue, light intensity, foliar pruning, crop maturation, and the stimulus of certain agricultural chemicals. The mechanisms of temporary resistance which control the development of the pathogen in the foliage of tomato and potato plants have not been determined. However, the factors which change this resistance are those which have a common effect on the physiology of the host.

The effect of age on the resistance of foliage is clearly demonstrated by inoculating young plants and determining the degree of disease development on the individual leaves in a given period of time. Infection in the topmost and youngest leaves is often macroscopically invisible and rarely exceeds a minute necrotic fleck under normal conditions. Meanwhile, infection in the lowermost and oldest leaves produces extensive necrosis and chlorosis, oftentimes causing wilt-like collapse and defoliation. The temporary resistance of young leaves prevents the development of the disease, and the fungus persists in such tissues either as a suppressed parasite or in a completely dormant condition. The resistant mechanism disappears and the organism becomes pathogenic on maturation and aging of the leaf.

The physiological mechanism controlling temporary resistance in young foliage may be a defensive mechanism against toxins pro-

duced by the pathogen, a metabolic suppression of fungus development, or a combination of both processes. Sterile culture filtrates of *A. solani* f. *dauci* are toxic to tomato plants and produce symptoms of epinasty, chlorosis, and necrosis which are similar to the progress of the disease on old mature leaves. Brian et al (5) recently isolated a phytotoxic and fungitoxic compound from this fungus and have named it alternaric acid. Pound and Stahman (18) have demonstrated that similar symptoms are induced in tomato foliage by this compound and the toxic substances produced *in vitro* and *in vivo* by the pathogen. Toxins probably have a major role in the defoliation of the severely infected leaf; this process simultaneously removes a large source of toxin from the plant. However, culture filtrates of the pathogen appeared equally toxic to young and old tomato leaves. Therefore, the absence of severe toxin-induced symptoms in the young top leaves of foliage inoculated plants indicates little active toxin is present in these tissues.

The general metabolic change accompanying the aging of tissues is in the ratio of anabolism to catabolism. Assimilatory processes dominate the metabolism in young tissues, but as such tissues mature, the rate of anabolism steadily decreases. Senescence is characterized by catabolism exceeding anabolism. The disease develops most rapidly and destructively in host tissue where such a condition prevails.

The effect of light in the development of early blight infections also is related to the levels of tissue metabolism. The basic function of light in the photosynthesis of green plants influences all the assimilatory processes. Reduction of light intensity by shading decreases the rates of plant anabolism. Such low light intensities also decrease the temporary resistance of the tissues, permitting a more rapid development of the pathogen and a more rapid decline of the infected leaf. The effect is more noticeable in young than old foliage. Old tissues have already lost the defensive mechanism found in young tissues, therefore, the same physiologic process appears to be modified by low light intensities and aging to increase susceptibility.

Tissues which are growing rapidly have a high rate of assimilation and obtain many of their synthetic needs from adjacent mature tissues. The suppression of this drain of synthesized materials from mature leaves by pruning young leaves and buds on young plants results in less disease in the mature leaves. Similarly, the ripening of fruit on plants draws on the synthetic products of the foliage. Horsfall and Heuberger (10) demonstrated that the degree of disease development of tomato plants in the field was related to the number of fruits that were permitted to develop on the plant; i.e., the most resistant plants were those on which fruiting was completely prevented by defoliation. The demands of rapidly growing tissues for the photosynthetic products of mature tissues appear to lower the disease

resistance of the latter; when this process is retarded, susceptibility to disease decreases.

The changes found in non-reducing sugars within the maturing plant and accompanying the increase of disease appear to support this hypothesis. Sucrose, the principal non-reducing and storage sugar in green plants, was demonstrated by Went (27) to fluctuate with the synthesis and translocation of the carbohydrates within tomato plants; hence, the disappearance of this non-reducing sugar from the foliage extracts late in the season probably indicates that the demands of the ripening fruit are greater than the synthetic efforts of the remaining green tissue.

Simultaneously, disease became more severe on these plants and even the youngest leaves were heavily attacked. The disease further accentuated the unbalance of demand and supply between the fruits and the leaves by reducing the photosynthetic surface through 50 per cent defoliation of the plant. Therefore, the situation may be likened to a pathogenic chain reaction; i.e., the pathogen reduces the effective photosynthetic surface and less carbohydrates are available for the ripening fruit; consequently, the increased demand by the fruit for the non-reducing sugars available in the remaining healthy tissue results in the loss of its temporary resistance and in further defoliation by the pathogen.

Disappearance of the non-reducing sugars may have been affected by the metabolic activities of the pathogen, since it was present in all the leaves at that time. However, the increase in susceptibility affected by other factors which deplete assimilated food reserves indicate that the presence of the fungus in these tissues is the result and not the cause of loss of non-reducing sugar.

Two chemicals, 2,4-D and Phygon, increase disease development by suppressing the temporary resistance of the foliage. The carbohydrate metabolism of herbaceous plants is markedly affected by 2,4-D. For example, Rasmussen (20) found that the application of 2,4-D to dandelions resulted in an increase in reducing sugars, a decrease in non-reducing sugars and reserve carbohydrates, an increased respiration rate and an over-all loss in dry weight. Similar responses have been reported for the effect of 2,4-D on the annual morning glory by Mitchell and Brown (14) and on bean plants by Brown (6). Presumably, 2,4-D would have a similar effect on the physiology of potato and tomato plants; an identical pattern to the changes in carbohydrates found to occur in maturing field grown tomatoes. No evidence is available of the effect of Phygon on the physiology of plants, although the injuriousness of heavy dosages of this chemical to potatoes and tomatoes is well known. In all probability, this chemical increases the susceptibility to early blight by influencing the same metabolic balance.

Glucose and sucrose, the principal reducing and non-reducing sugars of tomatoes, are equally utilized at low concentrations for fungus growth and respiration; consequently changes of these sugars in host tissue are not directly effective in changing pathogen development.

The influence of these factors in increasing the development of early blight in potatoes and tomatoes has important practical implications. The vigorous development of early blight on shaded plants may explain the occasional severe epiphytotic of this disease such as that observed by Whetzel (26) in Bermuda. Although the disease is commonly encountered in a benign form as a gradually enlarging necrotic leaf spot which eventually causes the defoliation of the leaf, with the proper environmental conditions it may become as destructive as late blight caused by *Phytophthora infestans*. The requirements of saturated humidity and high temperatures were determined by earlier workers (12, 15, 19).

The present study demonstrated the fast rate of disease development under low light intensities, and the increased susceptibility of the young tissues under such conditions. Therefore, the low light intensities during a prolonged period of cloudy weather would be expected to have a similar effect. Such appears to have been the conditions in the aforementioned Bermuda epidemic. Whetzel (26) reported almost daily rain, abundance of lesions even on the uppermost young leaves, and stated that the attack was not associated with the maturity of the tops of the potato plants.

The effect of 2,4-D in increasing the susceptibility of host tissue to attack by *A. dauci* f. *solani* is important in view of recent attempts to use this hormone for weed control in potato fields. The potato plant has been demonstrated to be more tolerant than many weeds to 2,4-D; therefore, Thompson and Shuel (25) attempted to control weeds in potato fields with one application of the hormone after blossoming of the plants. The action of this chemical in reducing host resistance to early blight indicates that the simultaneous occurrence of the proper environmental conditions with the weed-killing treatment may result in a destructive epiphytotic of this disease.

SUMMARY

The pathogenicity of *Alternaria dauci* (Kühn) Groves and Skolko f. *solani* (E. and M.) Neergaard was investigated to determine the role of pathogenic virulence and host resistance in early blight, the defoliation disease of tomato and potato. An intensive study of 16 isolates of the pathogen collected in Minnesota and Rhode Island showed them to vary in the usual cultural characters, sporulation and

virulence. The races differed in the degree of relative virulence, and the order of aggressiveness was constant in comparisons on different host and tissues.

Two types of host resistance, permanent and temporary, have a role in the development of early blight. Permanent resistance is governed by genetic factors. Tests of four species of *Lycopersicon* showed such resistance to be greatest in *L. hirsutum* and least in *L. pimpinellifolium* of the selections tested.

Temporary resistance exists in the young foliage of growing solanaceous hosts and is governed by physiological factors within the plant. The disease developed vigorously and killed many of the old leaves of inoculated young plants within a week under optimum greenhouse conditions. Many of the topmost leaves of the same plants appeared disease-free although careful examination revealed numerous, minute necrotic flecks. The organism was isolated from other young leaflets which showed no macroscopic symptoms of infection. Alteration of host physiology by increased age, crop maturation, reduced light intensities and certain chemicals (sodium 2,4-dichlorophenoxy acetate and 2,3-dichloro-1,4-naphthoquinone (Phygon)) increased the amount of disease on greenhouse-grown tomatoes and potatoes. The effects of such agents were most marked on young resistant foliage. Conversely, suppression of growth in young plants by removal of growing points and young leaves decreased the susceptibility of the mature leaves.

The symptoms of epinasty, wilting, chlorosis, and necrosis produced on severely infected mature leaves were induced in young tomato plants when cut stems were immersed in culture filtrates of virulent and avirulent races of *A. dauci* f. *solani*. Young and mature leaves were equally affected, but the effect of such toxins on the temporary resistance of young leaves was not determined.

The reducing and non-reducing sugar content of tomato plants maturing in the field was studied in the latter part of the season as early blight became epiphytotic. The non-reducing sugar content of the tissues became negligible and the reducing sugars increased as most of the fruit ripened and the plants became completely infected by the pathogen. The weight of the mycelial mat produced by *A. dauci* f. *solani* grown in tissue extracts from young resistant leaves was less than in similar extracts from old susceptible leaves. Comparison of weights of mycelial mats produced by virulent and avirulent races of the pathogen grown on media containing equal amounts of carbon as glucose and sucrose showed no marked differences in the utilization of these sugars. It is concluded that the temporary resistance of young tissue to *A. dauci* f. *solani* is related to carbohydrate metabolism, although the exact mechanisms involved remain unknown.

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